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THE ANATOMY OF THE ADULT QUEEN AND WORKERS OF THE ARMY ANTS *ECITON BURCHELLI* WESTWOOD AND *ECITON HAMATUM* FABRICUS

ROY M. WHELDEN

[CONTINUED]

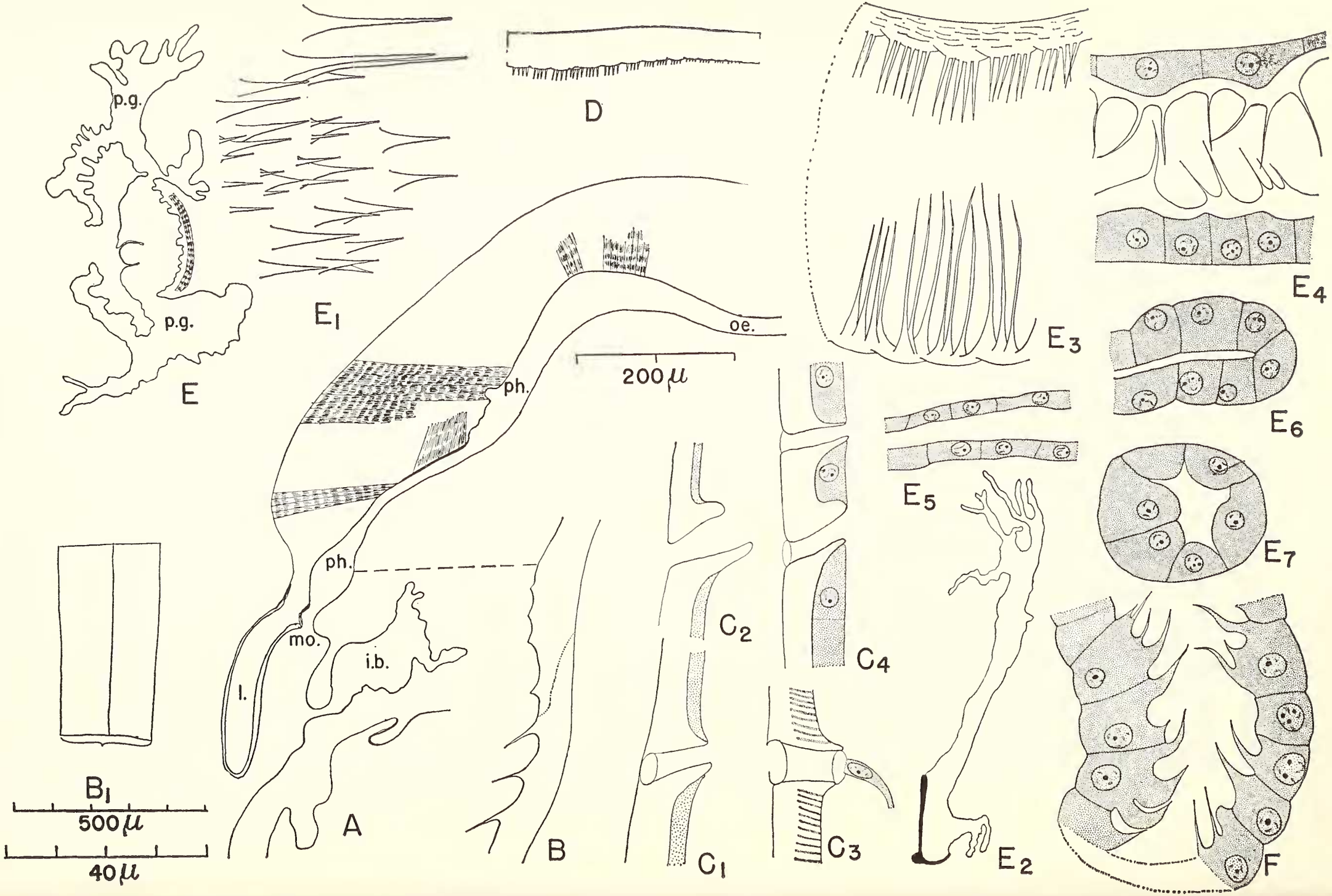
Basically the pharynx of these two ants is a large, flexuous tube more or less parallel to the frontal surface of the head. Its walls give the impression of variability of structure since even the smallest variation in the angle or in the region of sectioning can produce a striking difference in appearance. Despite the appearance of rigidity of the thick, darkly pigmented wall, this wall is probably flexible and elastic, which may also cause changes in appearance. What follows is to be considered only as a description of its appearance, subject to variation in dimensions and outline.

The lowest portion of the dorsal wall is similar to the wall of the buccal tube which it adjoins, but the spines from its inner surface are much finer. These spines occur for a short distance

only, usually gradually decreasing in size until replaced by low transverse ridges which are present in gradually decreasing size until they cease (Fig. 4, A, B), before the midpoint in the pharynx. Often there is a long portion that is smooth. Beyond this mid-point, fine spines appear in transverse rows (Fig. 4, D). These spines vary in length, though always short, as far as to where the pharynx bends strongly backward; from this point on to the beginning of the oesophagus, the spines on the upper surface are much longer and less obviously in rows (Fig. 4, E_3). Throughout its length this dorsal wall of the pharynx is strongly pigmented.

A series of transverse sections of the pharynx of a queen of *E. burchelli* (Fig. 5) shows the difference possible upon sectioning at different levels or at an angle. Where the diverticulum of the maxillary gland occurs, a transverse section shows the dorsal wall uniformly thin, contrasting sharply with the thicker more heavily pigmented ventral wall (Fig. 5, A). In the region above the maxillary gland, both the dorsal and the ventral wall of the pharynx also show changes. The dorsal wall is strongly arched upward in the middle area and very thick, gradually narrowing towards its lateral margins, where it turns suddenly outwards and abruptly becomes thin (Fig. 5, B). From the central arched area, a broad muscle mass extends to the dorsal wall of the anterior head region. Two large muscle masses occur, one on each side of the central mass; which more or less parallel the pharynx. The ventral wall of this part of the pharynx ends laterally in large cylindrical masses, deeply pigmented. In more posterior sections a gradual thinning of the dorsal wall is seen with an accompanying narrowing of the central muscle mass. Where the thickening of the dorsal wall ends, a new muscle mass occurs (Fig. 5, C). This is attached to the central (thickest) part of the wall and passes upwards, dividing the muscle first mentioned above into two narrow parts. This central muscle gradually increases in size as it passes upwards to its central attachment to the mid-frontal wall. The two large lateral muscles accompany the central one. The thickness of the dorsal wall continues uniform for the rest of the length (Fig. 5, D to H, inclusive).

The ventral wall gradually changes in the lateral margins of the thickened region, the cylindrical form becoming rapidly


p.g.
p.g.
E
E1
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l.
A
B1
500 μ
40 μ
B
C2
C1
C4
C3
E3
E4
E5
E6
E7
E2
F

smaller, with upcurved narrowing flanges to nearly the posterior end of the pharynx (Fig. 5, D through H), where they gradually fade as part of the wall of the post-pharyngeal gland chamber (Fig. 5, I, J).

The inner surface of the ventral wall of the pharynx has a short area thickly armed with coarse forward-directed spines which gradually decrease in size near their upper limit. After this the ventral wall is smooth for most of its length and is characterized by the occurrence of about twenty large pits, in four irregular rows of five each. In the queens, each of these pits is about 8 μ in diameter and nearly cylindrical; often the wall projects outward around the base of the pit, forming a projecting ring (Fig. 4, C_{1-4}; Fig. 5, M_{1-3}). A thin membrane closes the inner end of the pit; in or near the center of this membrane, a minute conical papilla occurs. In workers, the wall of this part of the pharynx rarely exceeds 5–6 μ in thickness. Here the pit projects from the pharynx wall forming a stout collar nearly 10 μ high. The wall of the collar is 2–3 μ thick.

Into each of these pits, a slender nerve fibre enters and passes

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FIG. 4. The pharynx and pharyngeal gland.

A Semidiagrammatic pharynx and associated parts: l = labrum; mo = mouth; i.b. = infrabuccal pocket; ph = pharynx; oe = oesophagus

B Ventral wall of pharynx, near mouth. Dotted line: junction of pigmented wall (above) and colorless wall (below)

B_1 Dorsal wall, showing relative thickness or two layers

C_{1-4} Ventral wall, showing large pits in posterior half of wall in queen

D Dorsal wall of pharynx, near junction with oesophagus

E t.s. anterior oesophagus, with lateral chambers of post-pharyngeal gland (p.g.) in queen

E_1 Inner surface of wall of these chambers, showing long spines

E_2 Chamber of pharyngeal gland

E_3 Wall of main branch of chamber of pharyngeal gland, near oesophagus, showing transverse rows of long spines

E_4 Branch of pharyngeal gland, transitional between chamber and secretory portion

E_5 l.s. of pharyngeal gland of worker, near base of branch

E_6 l.s. end of branch of queen pharyngeal gland

E_7 t.s. of queen pharyngeal gland, near end of branch

F l.s., secretory branch of the male pharyngeal gland

Scale: E and E_7—500 μ scale; others—40 μ scale


500 μ
50 μ
ap.
n
M1
M2
M3
p.g.
p.g.
G
ch.
K
L
C
ch.
F
E
oe.
ch.
B
m.gl.
A
D
ch.
ph.
ch.
H
oe.
p.g.o.
p.g.o.
ph.
I
ch.
J

upwards, occasionally free in the central region, frequently near or against the lateral wall, and ends just beneath the small conical papilla (Fig. 5, M_2, M_3).

Relatively small muscles pass from the ventral wall of the pharynx to the inner surface of the upper end of the large tentorium projecting upwards from the ventral wall of the head (Fig. 5, C, ap). Another slender muscle extends posteriorly from the wall of the pharynx through the brain parallel to but below the oesophagus and to end in the posterior wall of the head. This muscle varies considerably, especially in the queens. It may be formed of eight separate heads inserted into a single slender tendon or frequently fewer heads with a single muscle mass at the point of its origin near the neck opening.

The transition from pharynx to oesophagus is not sharp, and occurs at some distance posterior to the prominent bend in the pharynx. The oesophagus varies between the various forms and in various regions in a single individual. Characteristically, it is a straight tubular organ, the inner surface of which is abundantly armed with long, acute spines, usually directed forward (Fig. 3, C_2). These spines, conspicuous in queens, measure from 20 μ to 35 μ in length. Yet occasional individuals lack spines on the inner surface of the oesophagus or have spines in limited regions. Smoothness of the oesophagus wall is commoner in soldiers than in other forms. Individuals occur with the oesophagus free from spines only in the thorax, or in the anterior portion of the

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FIG. 5. Pharynx of *E. burchelli* queen (series of tranverse sections about equal intervals): pigmented portion of wall shown in solid black. Figures oriented with dorsal wall below.

A Just above mouth, beyond area of bristles surrounding mouth cavity, maxillary gland (m.gl.)

B–G Changes in extent of pigmented portion of wall, details of dorsal wall in D and G (in C, nearby nerve (n) apodeme (ap) and muscles, body wall (ch.)

H Anterior end of oesophagus (oe), upper end of pharynx (ph)

I Junction of pharynx with oesophagus

J Apex of pharynx with edge of openings of pharyngeal gland (p.g.o.)

K Extent of chamber of pharyngeal glands (p.g.)

L Dorsal wall of I

M Several pits in posterior part of ventral wall

Scale: L_1, M_1, M_2, M_3, D and G = 50 μ scale; others = 500 μ scale

thorax, or only in that part of the oesophagus which is overlapped by the brain. When present, the spines frequently occur singly; less frequently in transverse rows of four to six spines. Often these rows of spines occur only on the dorsal wall, the opposite wall being smooth. When spines occur over the entire surface, those on the ventral surface may be 35 μ long, while on the dorsal surface they measure less than 12 μ.

Surrounding the oesophagus from one end to the other, is a loose network of muscle fibres that may be vaguely separated into two layers. In these the fibres are so irregularly arranged that longitudinal and circular layers are difficult to distinguish. (Fig. 3, C_{1-3}).

A large irregular opening through the lateral wall of the oesophagus, posterior to the transition from pharynx to oesophagus, leads into the chamber of the post-pharyngeal gland. Structurally it is the same in the queen and all worker forms; yet its form seems to be different. In the queens, the gland is large, by far the largest object in the head; its many branches extend over the brain and even back of it, fill much of the space between the brain and the lateral walls of the head, and form a dense mass anterior to the brain. So large is it that the mandibular muscles, the largest found in the head, are reduced to thin plates against the lateral wall. In workers, this gland is much smaller, with relatively few branches, most of which occur anterior to the brain. In soldiers, this gland is formed of a few well-separated slender branches, some above and some lateral to the brain, but not near it, and some shorter anterior branches.

These branches arise from the walls of a large chamber, which in the queens is irregular in shape, and with several coarse irregular branches (Fig. 4, E_2; Fig. 5, K). The chamber walls are thick, uneven, and bear internally many rows of long acute spines, measuring 30–45 μ in length. These spines usually occur in rows of four to six, those in each row about equal in length (Fig. 4, E_3).

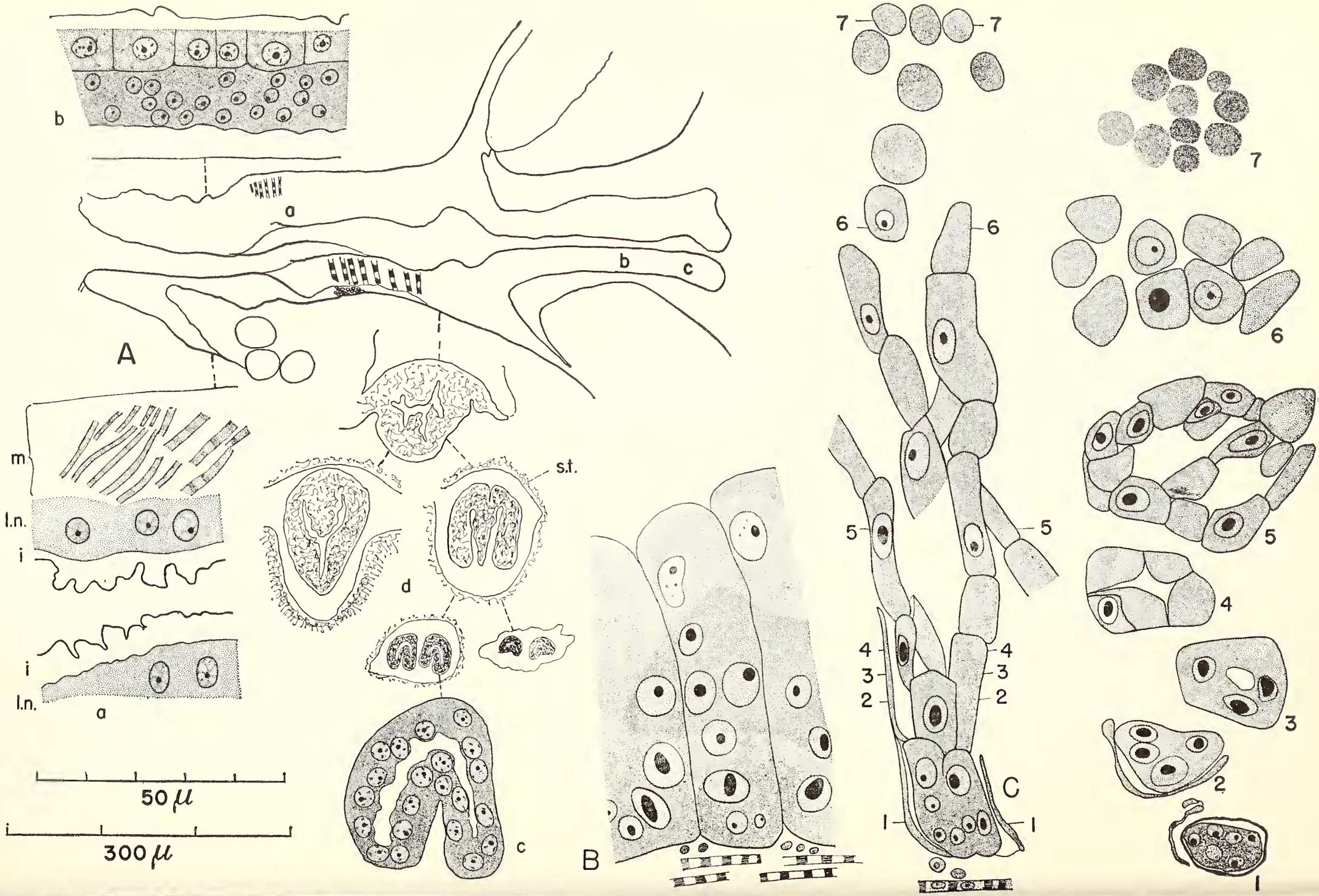
The secretory branches arising from the walls of the main chamber and from its several coarse, often long branches are uniform in size and appearance. In the queens, the average diameter is 15–18 μ, with the central lumen 2–3 μ in diameter (Fig. 4, E_{4-7}). In all workers, these branches are usually larger than those in the queens, having a diameter of 18–24 μ, with that

of the central lumen 5–6 μ; infrequently, this central lumen may be as much as 12 μ in diamenter, especially near the base of the branch. In males, the branches of this gland are generally smaller, averaging about 12 μ in diameter, with a lumen 3–4 μ in diameter. Frequently, the lumen is larger, with many large curved spines projecting into it. These spines are thin-walled, with cytoplasm reaching far into the center of the spine. The small spherical nuclei occurring in the secretory branches measure 3–4 μ in diameter (Fig. 4, E_4, F).

The small crop of the queens in found in the anterior part of the first gastric segment; in the workers, it occurs near the mid-portion of the first segment. In either form, the wall of the crop is thin and has a few small discoid nuclei. Muscle fibres are either completely absent from the wall of the crop or occur sparingly.

The proventriculus, like the crop, is small, more so in the queens than in the workers. Its structure is identical in all forms. The anterior and posterior parts are separated by the junction of the proventriculus to the anterior end of the wall of the stomach (Fig. 6, A). The anterior part is larger, especially in the workers. In the workers, the longitudinal axis of the two parts forms a straight line; in the queens, this occasionally occurs, but often the anterior part forms a sharp angle (about 80°) with the posterior part. This may be a result of the rhythmic change from contraction to physogastry.

The anterior part of the proventriculus varies in length from 400 to 550 μ, with a maximum diameter from 120 to 180 μ. As a rule the greater lengths occur with the smaller diameters, perhaps an indication of variation in shape as well as in position during physogastry. Four distinct layers of tissues form this anterior part. The innermost is a colorless featureless wall from 3 to 8 μ in thickness; the inner surface of this layer is much wrinkled (Fig. 6, A–a). External to this inner layer, is a unicellular layer 6 to 14 μ thick. This layer may be compared with the hypodermal layer of the external wall. Surrounding this is a much thicker layer of muscle fibres sometimes circular, but often almost radial, due to the irregularity of the wall and consequent variation in the angle of cutting. External to this is the fourth layer, much thinner than any of the other three and composed of longitudinal muscle fibres. Finally, there is a thin featureless wall external to these longitudinal fibres.


b
a
b
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m
l.n.
i
i
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a
s.t.
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c
50 μ
300 μ
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7
7
7
6
6
6
5
5
5
4
4
3
3
2
2
C
1
1
1

Transverse sections of this anterior part of the proventriculus show clearly the four layers described above and also show the muscle fibre variability of the third layer. Also shown is the variable nature of the central lumen. Sometimes this central lumen is large and almost cylindrical, the enveloping wall being uniformly thin. Or the wall is so collapsed that the central lumen is almost obliterated, there remaining only a small central portion from which three or four irregular, unequal narrow arms radiate. In a single insect, the lumen varies from one level to another, measuring as much as 24 μ in maximum dimensions at one level and less than 8 μ at a level only slightly distant from the first.

At the point of contact with the wall of the stomach, the stomach becomes thin, with irregular small cells comprising it; similarly the cells of this part of the proventriculus become small and more or less uniform in structure.

The posterior proventriculus, within the anterior end of the stomach, is more or less surrounded by the thick walls of the stomach, but is never in contact with them. This part is smaller than the anterior part, measuring 250–270 μ in length (rarely more) and 80–120 μ in maximum diameter. The cells are more uniform than those in the anterior portion, with muscle fibres mostly lacking except in the basal region. Transverse sections (Fig. 6, A–d) show the great change from one point to another of this posterior region. Particularly noticeable is the change in the outline of the central lumen, which invariably shows many narrow radiating arms. For more than half its length, this posterior part tends to be more or less cylindrical, though

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FIG. 6. Proventriculus and ventriculus.

A Outline of proventriculus
- a. l.s. of mid-portion of wall of main body, showing irregular muscle layer, (m) surrounding layer with large nuclei (l.n.) surrounding thick intima (i)
- b. l.s. of wall, proventriculus valve
- c. t.s. near tip of proventriculus, one half only
- d. Sections of valve of proventriculus and inner margin of stomach (st.)

B Cells and muscle layer of stomach wall of worker

C Cells and muscle layer of queen stomach wall with t.s. numbered to show approximate location in wall

Scale: A,a,b,c,B and C = 50 μ scale; A_d = 300 μ scale

occasionally somewhat compressed laterally. At some point near or posterior to its mid-point, the transverse section becomes vaguely like an inverted letter W in shape; then separated and the resulting transverse section resembles two irregular inverted U's which gradually decrease in size (Fig. 6, A–c, d).

The cells forming this part of the proventriculus are in two distinct layers, with a thin featureless inner membrane surrounding the central lumen (Fig. 6, A–b). The inner layer is formed of uniform prismoidal cells, similar to the hypodermal cells. Around this, there is a thicker layer of small irregular cells, the separating membranes of which may rarely be discerned. In this layer, thick near the anterior proventriculus, the number of nuclei gradually decreases, as does the thickness of the layer, which finally ends near the posterior end, leaving a small lumen.

In both its shape and the structure of its component cells, the stomach of the queen differs strikingly from that of the workers. In the queens, it is a more or less cylindrical body, 400–570 μ in diameter. In many individuals, the diameter is uniform from one end to the other; in others, the diameter varies greatly at different points. The anterior end is uniformly hemispherical; the posterior end varies, being short and conical in some individuals, in others drawn out into a gradually narrowing neck which may be as much as 400 μ long. This narrow portion may be in line with the main part of the stomach, or it may turn abruptly downward, in extreme examples at right angles to the main part of the stomach. The total length of the stomach, from the junction with the proventriculus to the beginning of the intestine, where the Malpighian tubules are found, varies from 2400 to 5000 μ. Variability in length is not correlated with the degree of physogastry; for of two individuals having stomachs almost equally short, one may be contracted and the other fully physogastric; two individuals with very long stomachs may also be one contracted and one physogastric. The stomach is not elastic in length.

In the workers, the stomach is always pear-shaped, and varies little in size in any single caste, but considerably from minor workers to the large soldiers. In the workers, the stomach wall is seldom more than 110 μ thick, always much less than the thinnest wall found in the queens.

In the workers, the cells of the stomach wall resemble those

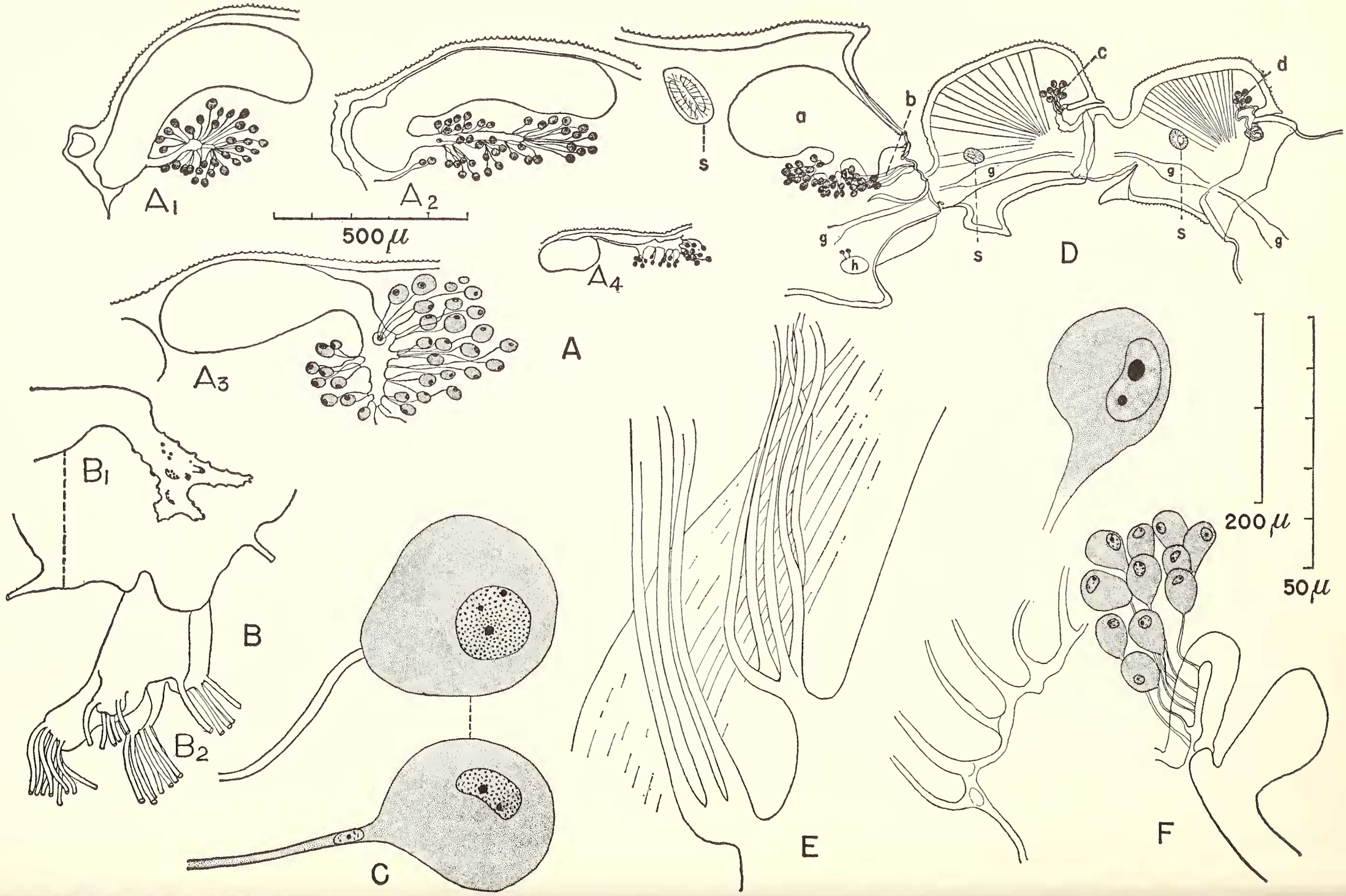
found in other ant species, being columnar and closely aggregated. In them, small nuclei occur at the base; above, larger nuclei occur haphazardly (Fig. 6, B). The cytoplasm becomes thinner and more vaculate from base to apex in these cells.

In queens, the structure of the wall of the stomach is different. In it, the cells do not form a uniformly compact layer. Instead, each cell is separated from its neighbors not only by narrow spaces, but by thin scale-like cells that completely or partially surround the basal unit and extend to the height of the basal unit which is a multinucleate columnar cell with distinct cell membranes (Fig. 6, C). Minute discoid nuclei occur sparingly in these scales. From the apex of the basal unit, secondary scales occasionally reach upwards but do not surround the secondary units of the stomach wall. Beginning with these secondary units, the wall breaks up into coarse filaments which at first surround a central open space of irregular shape. Progressing upwards, these filaments branch several times, forming irregular, usually two to three times compound, funnel-shaped tubes. Only near the inner surface of the wall do the filaments become separated, appearing in transverse sections as groups of irregular cells 10–14 μ in maximum dimension. Above these, are numerous small spherical bodies in the central lumen of the stomach which at first have a distinct external wall or membrane, but presently have a limited outer surface. Occasionally these spheres are found in abundance in the posterior end of the stomach lumen, absent in the extreme anterior end, but increasing in numbers near the posterior end. Such a wall structure effectively increases the functional cell surface of the stomach wall.

Externally there are usually two muscle layers, the inner one of fibres encircling the stomach, the outer of longitudinal fibres.

The remaining parts of the digestive system, the intestine and the rectum, appear elastic in the queens, elongating noticeably as physogastry increases and decreasing during contraction. In the intestine, the surrounding muscle layer becomes thin at the peak of physogastry.

Occurring at the anterior end of the intestine, the Malpighian tubules (Sixteen in workers and about thirty in queens), vary from 23 to 25 μ in minor workers, 25 to 27 μ in medium workers, 32 to 35 μ in large workers and soldiers. In the queens, greater variation occurs, the extremes being 36 to 60 μ. All measure-


A1
A2
500 μ
s
A4
a
b
c
d
g
h
s
D
A3
A
B1
B
B2
C
E
200 μ
50 μ
F

ments here are for the diameter a short distance above the base of the tubule; this diameter gradually decreases from base to apex. The central lumen varies even more; for example, in each of two queens both having a tubule with a diameter of about 60 μ, the diameter of the lumen in one is 20 μ, in the other 38 μ.

Contrasting sharply with the thick wall of the intestine, the rectum wall is very thin and shows conspicuous rectal papillae. In workers, there are usually three, rarely six; in the queens, frequently six, infrequently three. Viewed from the surface, these papillae are broadly elliptical, at times nearly circular; from the side, most of them have the upper surface parallel to the wall of the rectum; a small number have sloping sides that give them a conoidal outline. Their dimensions vary considerably, both between the several forms and between individuals of any single form; average dimensions are: minor workers, 170 by 120 μ; medium workers, 220 by 140 μ; major workers, 320 by 185 μ; and queens, 440 by 185 μ. In about one-sixth of the length

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FIG. 7. Glands of posterior thorax and petiole.

A Variations of metasternal gland, showing chamber, secretory cells, ducts and diverticulum into which ducts open (*E. hamatum*)

A_1 Metasternal gland of medium worker, with diverticulum opening near base.

A_2 Medium worker, with diverticulum opening near base. Two cells of nearby small (intermediate) gland, below chamber base

A_3 Large worker, with diverticulum from apex of chamber

A_4 Minor worker, with diverticulum from apex of chamber

B_1 Apex of diverticulum with duct openings

B_2 Duct openings with bases of ducts

C Secretory cells of metasternal gland, with nucleus on duct near secretory cell

D Posterior thorax, petiole and post-petiole, also anterior part of gaster (parts in sequence here, but not from single ant), metasternal gland (a), intermediate gland (b), gland in petiole (c) and in post-petiole (d)

E Openings of ducts of intermediate gland in posterior thorax, through membrane connecting thorax to petiole

F Gland at leg base, with ducts opening through membrane joining coxa to thorax, secretory cell (above) and duct openings (at left) of gland

Scale: A and D = 500 μ scale; B_1 and F (whole gland) = 200 μ scale; B_2, C, E, F (details) = 50 μ scale

of the posterior rectum and around the anus, the wall becomes thick, the greater part being circular muscles.

Within the rectum, and to a less degree in the intestine, several large irregular masses of fecal matter may be observed. These are colorless, but contain many small particles of solid matter, some of which may be the remanis of the small spheres cast off from the apical portions of the stomach wall.

GLANDS OF THE THORAX AND GASTER

Smallest of the thoracic glands are six plands in the ventral region, one at the base of each leg (Fig. 7, F). Each of these glands is just above the base of the leg, lateral and often slightly posterior to this base. The glands are small, composed of 5–6 cells in the minor workers, and 12–15 cells in the queens, the cells usually compacted in dense masses, but occasionally found loosely grouped. Variation in shape includes those nearly spherical to some elongate conoidal; sample measurements in queens are 5 by 45 μ (a small, narrow cell), 58 by 44 μ (a rotund example), 70 by 36 μ and 90 by 33 μ. In workers the cells are less than half as large. The nuclei vary even more than do the cells; spherical and 24 μ in diameter or discoid and measuring 28 by 21 μ, 22 by 14 μ, or 20 by 18 μ; to an irregular shape.

The ducts are nearly always short and irregularly curved, to provide for the movement of the legs. These ducts have uniform diameters of 1.3–2 μ; they flare conspicuously at their mouths. Mostly, the duct openings occur singly; rarely do two to four ducts open so closely together that their common openings form a deep invagination of the membrane. Over much of the membrane, which joins the lateral wall of the thorax to the base of the outer wall of the coxa, the external surface is uniformly covered by small mamillate bosses, each topped by a slender acute small spine about 1.5 μ long.

The large chamber of the metasternal gland is often visible through the wall of the posterior thorax, especially in lightly pigmented individuals. It is possible carefully to lift off the overlying body wall, exposing the smooth, often glistening outer wall of the chamber of the gland, closely pressed against but never adnate to the body wall.

In the two *Eciton* species considered here, the metasternal gland is formed of four clearly defined parts: the large chamber,

an irregular diverticulum, usually from some point of the wall of the chamber, the numerous secretory cells, and the ducts connecting these cells with the diverticulum (Fig. 7, A_{1-4}).

The shape of the chamber is partly determined by the latero-dorsal wall of the posterior thorax, against which it lies; its length is limited by the third thoracic spiracle and the trachea ending there. Rarely does the chamber extend to that point; usually it is much less, even to less than one-half that distance. Frequently the chamber is allantoid, with a uniform diameter; occasionally, it has a diameter nearly equal to the length, in which case it has a broadly ellipsoidal or nearly spherical shape. Average dimensions are: minor workers, 170 by 100 μ to 220 by 90 μ; medium workers, 510 by 110 μ; large workers and soldiers, 610 by 150 μ; and queens, 750 by 200 μ.

The diverticulum into which the ducts of this gland open may arise from any point on the inner or ventral part of the wall of the chamber or from the anterior end. In extreme examples, it may originate from the wall of the posterior thorax below the chamber opening or between this opening and the junction of the thorax with the petiole. It is always coarse, of irregular shape and usually bears several short coarse branches along its sides. Occasionally, four to six nearly equal short blunt branchlets occur at the apex of the diverticulum (Fig. 7, B, B_1). The length of the diverticulum varies greatly, and may best be given by comparison with the length of the chamber; a long example may be nearly twice the length of the chamber and a short one may be less than one-sixth its length. No individual was found to have two distinct diverticula, though in two individuals branching occurred so near the base that a casual glance would lead to the conclusion that two short diverticula were present. The opening of the diverticulum, like that of the chamber, is irregular, though usually approximating a broadly oval outline. Often there is considerable asymmetry, the diverticulum and the chamber on one side of the thorax being of different shape from that on the other.

The many ducts of the metasternal gland, one from each of the secretory cells, open variously into the diverticulum; occasionally, the openings occur singly, though these openings usually form rather obvious small irregular groups; often as many as twenty ducts open so closely together they form a coarse cribellum or

even a small secondary diverticulum at any point on the main one. Rarely does a duct open directly through the wall of the chamber, usually near the base of the diverticulum. The length of the ducts is determined by the position of the secretory cells.

These secretory cells (Fig. 7, C) vary in shape and in size as much as do the cells of the several glands of the head. The most frequent shapes vary from nearly spherical, measuring 150 by 145 μ, with a spherical nucleus 12 μ in diameter to others measuring 195 by 180 μ, 190 by 150 μ, or 180 by 100 μ. Extreme variants may measure 250 μ in length and only 60–65 μ in diameter; usually such extreme cells occur near the end or at the margin of a group of cells. The cells of this gland generally form a compact group of irregular shape; their number which varies from one form to another, is fairly constant within any form. In minor workers, in which the smallest cells are usually found, the total number is 120–180; in medium workers, 200–300; in large workers and soldiers, 300–500; and in queens, in which the greatest variation occurs, there are at least 800 secretory cells. These numbers are obtained by counting the number of duct openings.

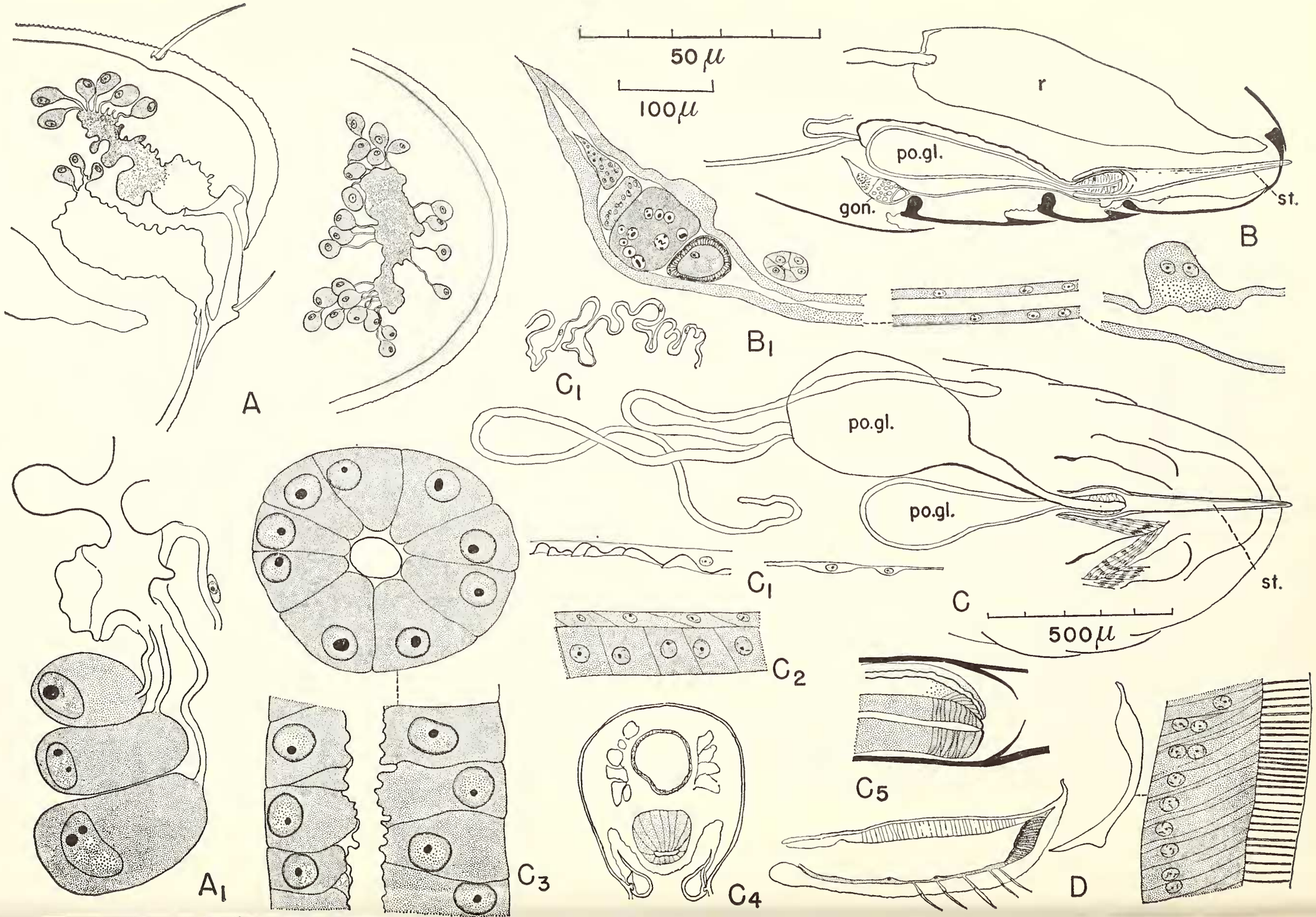
Another gland found in the thorax of the queens (Fig. 7, D, b) is a moderately large one, though small in comparison with the metasternal gland with which it is closely associated. It is scarcely possible to distinguish the cells of these two glands except by noting the opening of the ducts. In this second gland, these ducts open, usually in compact groups of three to eight (Fig. 7, E), through a membrane which connects the thorax to the petiole, near the lower part of the lateral wall. The secretory cells, numbering from thirty to fifty, or more, are mostly peripheral to the cells of the metasternal gland; although many occur within the aggregate of the metasternal gland cells, from which they may be distinguished only by the opening of the ducts.

A somewhat smaller gland occurs in the petiole of the queen; in this gland (Fig. 7, D), the openings of the ducts are always separate, and near the dorsal part of the membrane. In the workers, a much smaller gland occurs in the petiole and in the post-petiole; here the gland is much smaller, having six to twenty cells, the smaller number in minor workers, the larger in majors and soldiers.

Conspicuous among several large glands of the gaster of the queen are the paired glands analogous to those found in the petiole. Each of the segments of the gaster, including those telescoped together in the posterior part, contains a pair of these glands, which are smaller in the anterior segment than those in the following four segments. In the smaller telescoped segments, there is a progressive decrease in size. Each of these glands is found near the posterior edge of the segment and in the upper lateral region. In fully contracted queens, the secretory cells of the gland, one to several hundred in number, form a compact mass of irregular outline, 2–4 cells thick; in fully physogastric queens, these cells have been carried apart sufficiently to form a single layer of well separated, unevenly spaced cells. The cells vary in shape, some being nearly spherical, many being elongate conoidal or irregular, and a few—usually near the margin of the gland—being elongate and having a length three times their diameter. Dimensions of several cells are 60 by 33 μ, 50 by 41 μ, 40 by 34 μ, 38 by 33 μ, and 74 by 60 μ. Each of the cells narrows abruptly to a short duct 1.5–2 μ in diameter. In contracted queens, these ducts are contorted; in physogastric queens, they are nearly straight. They open separately through the intersegmental membranes.

The last pair of these glands, found near the base of the sting, in the irregular modified segment is smaller and more compact than any of the others. In this segment, deep in the posterior part of the gaster, a part of the cuticle is thick and strongly pigmented, contrasting noticeably with the thin, colorless, wrinkled membrane forming the greater part of its surface. In this segment, the ducts of this pair of glands open through the thick, pigmented wall and not through the thin membranous region.

In the workers of all forms, the gaster glands are reduced to two pairs, occurring at the extreme posterior end of the gaster (Fig. 8, A). The dorsal plate of the body wall curves down sharply, having an almost spherical surface. Below this and partially concealed by it, are two irregular plates which extend from the sides. These two parts, the large one and the smaller lateral ones, are joined by an extensive, somewhat wrinkled membrane forming a large irregular "cavity" opening ventrally. Beneath this, a second "cavity" is formed by a similar mem-


50 μ
100μ
r
po.gl.
gon.
st.
B
A
B1
C1
po.gl.
po.gl.
st.
C
500μ
C1
C2
A1
C3
C4
C5
D

brane. Through these membranes, the short and slightly irregular ducts of the two glands open. Each arises from a small (45 by 25 μ to 35 by 15 μ) cell; the number of cells of the upper (anterior) gland rarely exceed forty; those of the second gland are less numerous. In these glands, it is often difficult to separate the cells of one side from those of the other, the gland appearing to be a uniform mass extending from one side to the other.

In these glands the ducts and much of the "cavity" into which they open seem to retain the substance secreted by the cells of the gland—a uniform mass staining faintly by haematoxylin. The poison glands also have this property of retaining the secretion.

The two poison glands of the workers are unlike those of the queen, although fundamentally their structure is similar.

In all workers, the two poison glands are conspicuous, and the contents of the vesicle of the acid gland stains black. This gland, the larger of the two, varies even in workers of equal size. In some individuals, the vesicle is nearly one-third as long as

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FIG. 8. Reproductive system and glands in posterior worker gaster.

A Left: s.s., showing two glands and "pocket" with secretion. Right: l.s. larger gland (actually a pair) and "pocket" filled with secretion from gland cells

A_1 Larger gland, showing ducts and "pocket" portion

B Posterior of gaster, showing poison glands (po.gl.), sting (st.), reproductive system (gon.) and rectum (r)

B_1 Reproductive system: ovariole and oöcyte (left), oviduct (center), spermatheca and vagina (right)

C Posterior of gaster, showing poison glands (po.gl.) and sting (st.) with body wall outline (l.s.)

C_1 (above): median wall, partially empty acid poison gland. (below): left, wall of partially contracted gland, near gland base; right, wall of gland, distended and thin

C_2 l.s. of wall of alkaline gland

C_3 l.s. (below) and t.s. (above), anterior lobe of acid poison gland

C_4 t.s. sting, near base, showing openings of alkaline poison gland (below) and acid poison gland (above)

C_5 l.s. of sting base showing acid gland above, alkaline gland below

D Lobe of posterior gaster, ventral to genital opening, hypodermis and (right) detail of thickened hypodermis, posterior end

Scale: B and C = 500 μ scale; A, C_4, C_5 and D (outline) = 100 μ scale A_1, B_1, C_1, C_2, C_3 and D (detail) = 50 μ scale

the gaster; in others, it is less than half. In many individuals, it is a sack that gradually enlarges from the narrow tubular form as it emerges from the base of the sting, and reaches its maximum diameter near the broadly rounded anterior end (Fig. 8, B). In other individuals, it remains a narrow but gradually enlarging tube for nearly half its length, then enlarges abruptly to a broadly ovoid or even to a spherical pouch having a maximum diameter equalling approximately half that of the gaster (Fig. 8, C). The walls of this vesicle are usually thin, with thickened regions around the occasional small nuclei (Fig. 8, C_1); the thickness of the thin areas is from 1 μ in fully distended vesicles to 2–4 μ in others. In some individuals, the vesicle wall is much wrinkled; possibly as a result of repeated stinging. But individuals known to have used the sting just before being fixed show no such wrinkling nor any decrease in the contents of the vesicle.

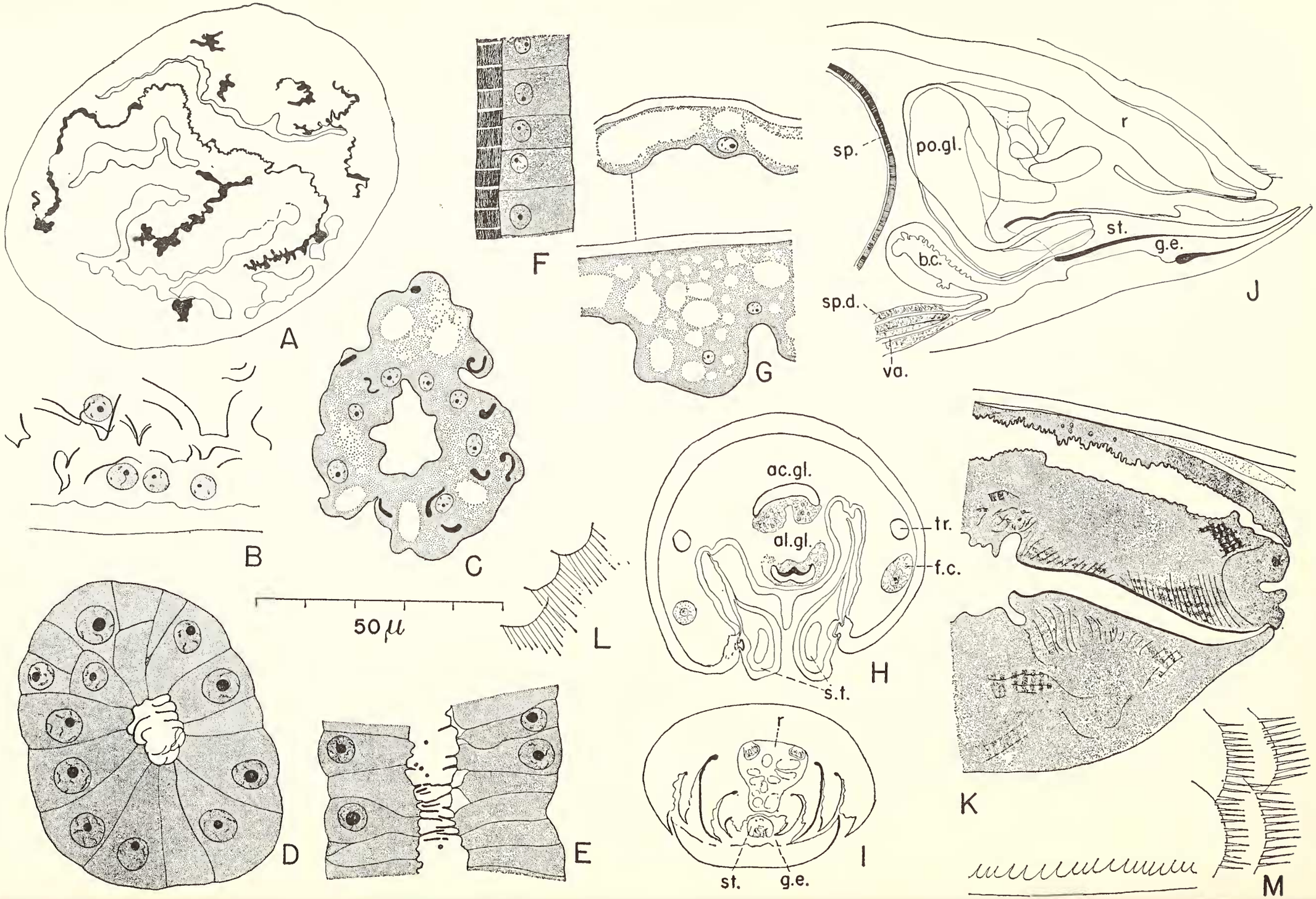
From the anterior end of the vesicle there arise two conspicuous cylindrical tubules, the secretory part of this gland. These tubules are long and often tortuous, conspicuously so in some workers. Ususally both tubes extend anteriorly for some distance; then one of the tubules turns abruptly posteriorly, passing back beside or above the vesicle. The second tubule usually extends much beyond the other, even to a point near the anterior end of the gaster, before turning posteriorly. In many individuals one of the tubules forms a tangled mass of a compact nature, anterior to and above the end of the vesicle. Occasionally, both tubules form a tangled mass anterior to the vesicle. The diameter of the tubules varies according to the worker form in which it occurs, from 20 μ or even less in small workers, to as much as 60 μ in large workers. The cells of the tubules are wedge-shaped (= cuneiform in sections), with uniform cytoplasm and subspherical nuclei 6–10 μ in diameter (Fig. 8, C_3). These cells surround a lumen made conspicuous by the thick sharply defined membrane, often strongly wrinkled circumferentially. Usually the cells of the tubule are pressed tightly against this membrane; but in some workers there is a considerable space between the membrane and the inner end of the cell; in such individuals, observation shows that there will be a slender tube extending from the surface of the cell to the membrane; in such individuals, careful examination of sections tangent to the sur-

face of the membrane will usually show small circular areas which seem to be finely porous, very thin areas rather than actual pores. These are best seen in occasional specimens in which a faint stain has been retained in these areas (Fig. 9, E).

The second (alkaline) poison gland is structually unlike the first, and is much smaller. Its wall is usually formed of two layers of cells; the outer layer being of thin uninucleate cells 1.5–3 μ thick, the inner of larger cells, 8–16 μ thick, with spherical nuclei much larger than those in the outer layer (Fig. 8, C_2). Comparison of the alkaline poison glands of many workers shows great variation in the outer layer, which may be uniform over much of the surface, or may occur over only a portion of the surface and be irregular, or may be completely absent. This may be comparable to the muscle layer that occurs in the queens.

As the two poison glands pass into the base of the sting, they narrow to slender tubes ending anterior to the lamellae of the gorgeret (Fig. 8, B, C, C_5). Invariably, the opening of the acid gland is above that of the alkaline gland; in rare cases, they may be asymmetrical, the acid gland opening being lateral to the alkaline. In nearly all cases, the acid gland opening is a flattened, transversely elongate slit which, by a turning down of the end of the gland, comes to be just over and very close to the very similar opening of the alkaline gland. The walls surrounding these openings are thick and formed of irregularly radiating tissue that even in the absence of discernible striations may be muscular. This tissue is much thicker around the alkaline gland (Fig. 8, C_4, C_5).

In queens as the two glands extend from the base of the sting, each turns upwards almost at once, at the same time separating, one going to one side, the other to the opposite side (Fig 9, J). This is necessitated by the presence of the large spermatheca forming an effective barrier to anterior elongation, and to a lesser degree by the large bursa copulatrix. Dorsally and laterally the large rectum centrally and the several glands and muscles laterally limit the enlargement of the poison glands. Due to these limitations, the glands tend to bend backwards, becoming irregularly twisted as they approach mature size. The "anterior" lobes of the acid gland become even more compressed, sometimes lying just posterior to the wall of the spermatheca, where they may mingle with the spermathecal glands; or alongside the rectum, posterior to the vesicle of the gland.


A
B
C
50 μ
D
E
F
G
sp.
po.gl.
r
st.
g.e.
b.c.
sp.d.
va.
J
L
ac.gl.
al.gl.
tr.
f.c.
s.t.
H
r
st.
g.e.
I
K
M

The alkaline gland, often S-shaped, is a coarse tube of uniform diameter, with a wall of a single layer of large prismatic cells, 14–40 μ thick and outside this layer, a second layer, closely pressed against the first is a layer of distinctly striated muscle fibres, 5–8 μ thick (Fig. 9, F). The fibres are irregularly grouped but tend to be circumferential, and sometimes form two layers, one crossing the other at an angle of perhaps 30°. This muscle layer covers the entire gland, sparingly at the apex, uniformly over the entire body; and, as the opening in the sting is approached, becoming a vague, thick, irregular mass in which striated tissue is not always discernible. Where such tissue appears the component parts are variable in numbers, location, and distribution. The opening of this gland is a narrow crescent-shaped slit (Fig. 9, H).

Since space is limited, the two glands do not differ greatly in volume but the acid gland usually has greater bulk. Structurally, it is different from the alkaline gland.

The wall of the vesicle of the acid gland is simplest to describe

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FIG. 9. Poison glands of queen (except D and E = part of poison gland of large worker).

A t.s., apical part of acid gland
B Edge of gland, at lower level
C t.s. anterior lobe acid poison gland near apex
D t.s. and E l.s., anterior lobe acid poison gland large worker, cf. A and C
F l.s. wall of alkaline gland showing muscles and secretory cells (cf. Fig. 8, C_2)
G t.s. portion of wall of acid poison gland in callow queen
H t.s. base of sting—stylets (st.), fat cells (f.c.), trachea (tr.), acid (ac.gl.) and alkaline (al.gl.) glands
I t.s. posterior gaster, showing rectum (r), sting (st.), genital entrance (g.e.), bursa copulatrix (b.c.), vagina (va.) and spermathecal duct (sp.d.)
J l.s. posterior of queen gaster, rectum (r), poison gland (po. gl.), bursa copulatrix (b.c.), vagina (va.), wall of spermatheca (sp.) and spermathecal duct (sp.d.), genital entrance (g.e.), sting (st.)
K Posterior gaster showing openings of poison glands and ventral surface of genital entrance
L Spines of dorsal surface of genital entrance
M Spines of ventral surface of genital entrance

Scale: H, I, and J = partly diagrammatic and less than 50 μ scale
others = 50 μ scale

as it is in newly eclosed queens. There is a dark staining (with haematoxylin stain) surface layer, uniformly 2–3 μ thick. Internal to this, is a vacuolate layer containing a few small spherical to ellipsoidal nuclei irregularly spaced. The internal margin of this layer is sharply defined in these young queens (Fig. 9, G). This layer may be uniformly 8–15 μ thick over much of the vesicle surface; but more often the entire surface except near the base of the sting (Fig. 9, lower part) is formed of an irregular layer varying from only 6–8 μ thick, to as much as 50 μ thick in a nearby area. Hence the central lumen is variable in size and irregular in shape. Queens showing this structure in the acid poison gland are rarely found. The wall of this gland is an irregular compact mass, in which almost no central lumen can be found. Both transverse and longitudinal sections show numerous irregular narrow regions many of which contain a black-staining substance. This dark substance cannot have much volume because the regions containing it are so thin. The potency of this sting gland is limited. Actually, the wall of this gland grows so much, in so restricted a space, that it becomes a thick, complexly folded mass, so completely filling the available space that in unstained material the gland appears to be an almost solid mass. The outer surface is always smooth (Fig. 9, B).

The apical tubules of the acid gland are unlike those in the workers. They are comparatively short, irregularly contorted, tapering from the large basal diameter to a narrow apex. In these tubules, the structure varies much as does the wall of the vesicle. In young queens, transverse sections show an irregular outline, both of the exterior surface and of the sharply defined central lumen (Fig. 9, C). In the wall of thin cytoplasm are many large vacuoles in the outer zone, as well as many oddly shaped "linear" masses staining black with haematoxylin, and many spheroidal nuclei 3–5 μ in maximum diameter. As the queens mature, the structure of these tubules changes noticeably and the tubule becomes a compact mass of vacuolate tissue surrounding a vaguely defined central lumen (Fig. 9, A). This is especially so in the lower part of the tubule; the change is not so great towards the apex.

The two poison glands narrow gradually as they approach the base of the sting. Within the base of the sting, they usually become slender distinctly separated tubes, the acid gland above and the alkaline below, each surrounded at least in part by a com-

paratively thick mass of tissue, extensive in the alkaline gland, thin in the acid gland, especially on the dorsal surface. Only near their end do the two glands unite to form a nearly solid mass, much thicker below than at the upper part (Fig. 9, K). Near the apex much of this mass is formed of irregularly massed muscle tissue. The actual openings, narrow slits of crescent shape, are anterior to the lamellae of the sting sheath (Fig. 9, H).

AN ANNOTATED LIST OF THE LYCAENIDAE (LEPIDOPTERA: RHOPALOCERA) OF THE WESTERN HEMISPHERE

By William Phillips Comstock and Edgar Irving Huntington

[Continued]

schryneri, Incisalia polios Misspelling of *schryveri* Cross
Type Locality:
Location of Type:
Original Description: 1939, Zool. Record, vol. 75, p. 316 (London).

schryveri Cross, Frank C., *Incisalia polios*
Type Locality: Chimney Gulch, Colorado.
Location of Type: Cross Collection or Colorado Museum of Natural History.
Original Description: 1937 (July), Butterflies of Colorado, Proc. Colorado Mus. Nat. Hist., vol. 16, p. 20, no. 1 (Denver, Colorado).
Note: Probably a distinct species.
Synonyms: *schryneri* (Zool. Record).

scopas Godman, F. D. and O. Salvin, *Thecla*
Type Locality: Jalapa, Mexico.
Location of Type: British Museum (Natural History) (Schaus Collection).
Original Description: 1887 (September), Biologia Centrali-Americana, Insecta, Lepidoptera-Rhopalocera, vol. 2, p. 89, vol. 3, pl. 58, fig. 5 ♂ (London).

scoteia Hewitson, W. C., *Thecla*
Type Locality: Minas Geraes.
Location of Type: British Museum (Natural History).
Original Description: 1877 (January), Illus. of Diurnal Lepidoptera, vol. 1, p. 206, vol. 2, pl. 82, figs. 683, 684 ♂ (London).
Additional Reference: Druce, H. H., 1907 (June), Proc. Zool. Soc. London, p. 594 (London). (Makes *scoteia* a synonym of *panchaea* Hewitson.)

scudderii Edwards, William H., *Lycaena*
Type Locality: Lake Winnipeg, Manitoba, Canada (♂ and ♀).